DR. KIMBERLY J LA PIERRE (Orcid ID : 0000-0001-7056-4547)

DR. DANIEL STEPHEN GRUNER (Orcid ID : 0000-0002-3153-4297)

Article type : Articles

Running Head: Arthropod biomass, grazing and nutrients

Title: **Increased grassland arthropod production with mammalian herbivory and eutrophication: A test of mediation pathways**

Authors: Eric M. Lind[1†], Kimberly J. La Pierre[2,3], Eric W. Seabloom[1], Juan Alberti[4], Oscar Iribarne[4], Jennifer Firn[5], Daniel S. Gruner[6], Adam D. Kay[7], Jesus Pascal[4], Justin P. Wright[8], Louie Yang[9], and Elizabeth T. Borer[1]

[1] elind@umn.edu, seabloom@umn.edu, borer@umn.edu; Department of Ecology, Evolution, and Behavior; University of Minnesota, St. Paul, MN 55108

[†] Corresponding author

[2] Department of Biology; Colorado State University, Fort Collins, CO 80523

[3] LaPierreK@si.edu; Current address: Smithsonian Environmental Research Center, Edgewater, MD 21037

[4] juanalberti@gmail.com, osiriba@mdp.edu.ar; pascualjesu@gmail.com; Instituto de Investigaciones Marinas y Costeras (UNMDP-CONICET), Argentina

[5] jennifer.firn@qut.edu.au; Queensland University of Technology, Brisbane, Queensland, Australia

[6] dsgruner@umd.edu; University of Maryland, College Park, MD 20742

[7] basicadamkay@gmail.com; University of St. Thomas, St Paul, MN 55105

[8] jw67@duke.edu; Duke University, Durham, NC 27709

[9] lhyang@ucdavis.edu; University of California, Davis, Davis CA 95616

This submission is intended as an Article in Ecology.

Abstract:

Increases in nutrient availability and alterations to mammalian herbivore communities are a hallmark of the Anthropocene, with consequences for the primary producer communities in many ecosystems. While progress has advanced understanding of plant community responses to these perturbations, the consequences for energy flow to higher trophic levels in the form of secondary production are less well understood. We quantified arthropod biomass after manipulating soil nutrient availability and wild mammalian herbivory, using identical methods across 13 temperate grasslands. Of experimental increases in nitrogen, phosphorus, and potassium, only treatments including nitrogen resulted in significantly increased arthropod biomass. Wild mammalian herbivore removal had a marginal, negative effect on arthropod biomass, with no interaction with nutrient availability. Path analysis including all sites implicated nutrient content of the primary producers as a driver of increased arthropod mean size, which we confirmed using 10 sites for which we had foliar nutrient data. Plant biomass and physical structure mediated the increase in arthropod abundance, while the nitrogen treatments accounted for additional variation not explained by our measured plant variables. The mean size of arthropod individuals was 2.5 times more influential on the plot-level total arthropod biomass than was the number of individuals. The eutrophication of grasslands through human activity, especially nitrogen deposition, thus may contribute to higher production of arthropod consumers through increases in nutrient availability across trophic levels.

Keywords: arthropod community, grazing, nutrient limitation, structural equation model, Nutrient Network, secondary production

Introduction:

Human activity in the Anthropocene has resulted in changes to multiple global cycles and patterns of biodiversity (Rockstrom et al. 2009). Perturbations to the global nitrogen (N) and phosphorus (P) cycles exceed those of global climate change so far, and human activity has created novel associations of plants and animals around the world (Steffen et al. 2015). The consequences of these alterations for the functioning of unmanaged ecosystems is not well understood, especially with respect to consumers (Throop and Lerdau 2004). Grazing by mammalian herbivores, domesticated and wild, is predominant feature of the grasslands biome, which also contains an evolutionarily unique set of arthropod consumers (Tscharntke and Greiler 1995). Alterations to grazing assemblages and nutrient availability are occurring in grasslands worldwide, as consequences of human activity. However, predicting responses of higher trophic levels to these changes is not straightforward given the complex responses of the primary producers, and the multiple pathways of influence between producing and consuming communities (Figure 1).

We take consumer, or secondary, production as an ecosystem-level descriptor of community response to changes of interest. The concept of "secondary production" can encompass a variety of ideas and empirical measurements, though typically invoked in marine and freshwater ecology contexts (e.g. Polis et al. 1997). Herein we use the term *sensu lato* to mean the mass of consumers, regardless of their higher trophic level. We are focused on how the size of the community of arthropod consumers, quantified here by biomass, is impacted by the changes to primary producing ecosystems arising from increased nutrient supply and altered grazing regimes.

Numerous empirical studies show altered arthropod abundance, biomass, and diversity with eutrophication, but most lack the data to isolate plant productivity, structure, plant community composition, and chemical composition or defenses as processes that drive arthropod community responses (Gruner and Taylor 2006, Poelman et al. 2008, Wimp et al. 2010, Rzanny et al. 2013).

Because each of these characteristics of the primary producer community can respond to both eutrophication and mammalian herbivory, multiple hypotheses form an interwoven set of pathways to predict arthropod biomass. Figure 1 summarizes the demonstrated and hypothesized pathways by which secondary production may respond to plant community changes in response to anthropogenic factors and mammalian grazing. We elaborate on each link below, with hypothesized relationships indicated by letters corresponding to the paths in Figure 1.

Nutrient availability impacts. In grasslands, the initial response to increased availability of nutrients such as nitrogen (N), phosphorus (P), potassium (K), sulfur (S) and other micronutrients is an increase in primary production as nutrient limitation is alleviated (Borer et al. 2014a, Fay et al. 2015; Figure 1 A). Temperate grasslands are thought to be especially nitrogen-limited (LeBauer and Treseder 2008) and there is substantial evidence for alteration of plant production due to anthropogenic increases in N (Stevens et al. 2015). However, previous work (Olff and Pegtel 1994) as well as recent meta-analyses and experimental evidence from a diverse set of grasslands indicates that co-limitation of production by multiple-nutrients (including P and K) is widespread (Elser et al. 2007, Fay et al. 2015). Because multiple nutrient limitation can create multiple gradients along which species can specialize, thus promoting coexistence (Harpole and Tilman 2007), a second generalized consequence of increased nutrient availability is reduction in local plant diversity (Clark and Tilman 2008, Borer et al. 2014a, Harpole et al. 2016; Figure 1 B).

The biomass of primary producers is thought to control biomass of consumer communities (McNaughton et al. 1989, Cebrian 1999, Cebrian 2004). An important consideration is that this increase in consumer biomass could be driven by increasing size of consumers, increasing abundance of consumers, or both (Cebrian 2015; Figure 1 C, D, E). At a local, plot-level scale in grassland systems, empirical evidence supports both mechanisms: plant biomass controls arthropod biomass through increases in mean size (Borer et al. 2012; Figure 1 C), and by increased abundance across all arthropod trophic levels (Wimp et al. 2010; Figure 1 D).

Manipulative experiments have demonstrated that arthropod diversity, abundance, and interactions can be controlled by plant diversity (Haddad et al. 2009, Scherber et al. 2010, Borer et al. 2012, Rzanny et al. 2013). However, few investigations have explored whether plant diversity leads to increased secondary production. Borer et al. (2012) sampled a long-running plant biodiversity experiment and found that plant biomass, which increased in plots with higher plant diversity, generated increased arthropod biomass, leading to higher arthropod diversity. This suggests plant diversity impacts on arthropod diversity result from a "sampling effect": with a greater abundance of consumers, the chance of including additional species increases (Borer et al. 2012; Figure 1 F). With respect to arthropod abundance and body size, with increased plant diversity, Haddad et al. (2009) demonstrated opposing relationships for herbivores (which decreased) versus predators (which increased). As arthropod herbivores are typically larger than arthropod predators this could potentially result in a negative influence of diversity on overall arthropod mean size (Figure 1 G).

Non-consumptive aspects of the plant community can also alter arthropod community structure. In grasslands, prior plant production accumulates as a thatch layer which can create architectural complexity and increase heterogeneity. This plant structure (as distinct from production of live biomass) can impact arthropod trophic dynamics, especially by easing intra-guild predation leading to more predation on herbivores (Finke and Denno 2002). Increased coexistence of consumers has also been shown to depend on architectural structure (Janssen et al. 2007). The consequences of these dynamics for overall arthropod biomass are less clear, but as herbivores compose a greater fraction of consumer biomass, increases in predation with more plant structure might suggest a decrease in mean consumer size (Figure 1 H) but an increase in arthropod abundance (Figure 1 I), with mixed consequences for total arthropod biomass.

The final hypotheses of primary producer control of arthropod biomass relate to the biochemical composition of the plant tissues, encompassing both defensive secondary chemistry and nutrient

availability and stoichiometry. Grasses are thought to be lower in defensive secondary compounds than eudicot lineages, although they contain relatively high concentrations of silica as a physical defense, and grassland herbivory includes a high proportion of piercing-sucking insects (e.g., Hemiptera: Auchenorrhyncha) which may be less susceptible to foliar secondary chemistry (Tscharntke and Greiler 1995). Increasing plant nutrient composition (as either nutrient quantity or ratios among nutritional components) is expected to lead to higher local abundance of herbivores (White 1984, Joern et al. 2011; Figure 1 J) and increased mass of individual herbivores (Awmack and Leather 2002; Figure 1 K). This increased abundance, however, may not necessarily lead to higher biomass, as Gruner and Taylor (2006) found fertilized plants supported a numerical increase of small-bodied juvenile herbivores and a shift to smaller species overall. Likewise, increased abundance is not necessarily reflected in interaction rates (e.g. herbivory) if there is a trade-off between abundance and feeding rate on plants with higher nutritional quality (La Pierre and Smith 2015). Finally, analogous to multiple co-limitation of plant communities, nutrients beyond nitrogen and phosphorus may control arthropod biomass. Sodium (Na) in particular has recently been implicated in this role (Kaspari et al. 2017).

Large mammal herbivory impacts. While large mammals can directly supply food resources to dung scavengers and parasites, their effects on foliar arthropod abundance are likely to be largely negative, via trampling or consumption (van Klink et al. 2015; Figure 1 L). Indirect effects include alteration of the abundance and identity of species in the plant community through selective grazing (Knapp et al. 1999, Foster et al. 2014; Figure 1 M, N), changes in physical environment including amount and structure of plant biomass, whether through consumption or trampling effects (Schrama et al. 2013, Figure 1 O), and increased heterogeneity at the habitat scale (van Klink et al. 2015). Where mammalian herbivory is high enough to create grazing "lawns," the remaining vegetation can increase in foliar nitrogen concentration (McNaughton 1984, Knapp et al. 1999; Figure 1 P). These effects are often dependent on the interaction between the grazer community, productivity, and plant community type (Cebrian 1999, Bakker et al. 2006). Because we hypothesize arthropod biomass is related to plant

biomass and plant diversity, and grazers can have a negative effect on the former and positive on the latter, the effect of mammalian herbivory on arthropod biomass may be contingent on which aspect of the plant community is a stronger mediator of the response (Figure 1).

We investigated whether soil nutrient availability and wild mammalian herbivory independently or jointly controlled arthropod consumer biomass (secondary production), using factorial fertilization, and fence-by-fertilization experiments replicated in 13 grasslands. Using identical field methods across a range of grassland environments, we asked: (1) What is the impact of soil nutrient availability on the secondary production of arthropod consumers? Is there evidence of multiple-nutrient limitation or co-limitation? (2) What is the impact of mammalian herbivores on secondary production of arthropod consumers? Is this modified by nutrient availability? (3) How does the plant community mediate these responses, e.g. through primary productivity, diversity, structure, or chemical composition?

Methods:

Experimental design: The study was conducted within two experiments conducted as part of the Nutrient Network (Borer et al. 2014b), the multiple-nutrient experiment and the fence-by-fertilization experiment. At participating sites, 5m x 5m plots were laid out randomly (and without respect to plant species identity) in locally homogeneous grasslands, typically in three blocks of 10 plots (10 sites with 3 blocks, two with 5 blocks, one with 6 blocks). In the multiple-nutrient experiment, three nutrient treatments (N, P and K plus micronutrients), each with two levels (control, added), were crossed in a fully factorial design for a total of eight treatment combinations per block. Nutrient addition rates and sources are: 10 g N m^{-2} $year^{-1}$ as timed-release urea [$(NH_2)2CO$], 10 g P m^{-2} $year^{-1}$ as triple-super phosphate [$Ca(H_2PO_4)_2$], 10 g K m^{-2} $year^{-1}$ as potassium sulphate [K_2SO_4] and 100 g m^{-2} of a micronutrient mix of Fe (15%), S (14%), Mg (1·5%), Mn (2·5%), Cu (1%), Zn (1%), B (0·2%) and Mo (0·05%). At some sites ammonium nitrate was used as a nitrogen source in treatment

year 1, but a separate experiment demonstrated equivalence for the plant community responses to these two N sources (Seabloom et al. 2013). N, P and K were applied annually; micronutrients were applied only once at the start of the experiment to avoid toxicity.

Fences were erected around the two remaining plots per block, one an unfertilized control plot and one with all nutrients added (NPK). The 230-cm-tall fences restrict access by mid-to-large-sized above-ground mammalian herbivores (>50 g). The lower 90 cm is surrounded by 1-cm woven wire mesh (hardware cloth) with a 30-cm outward-facing flange stapled to the ground to exclude digging animals (e.g. rabbits, voles), although not fully subterranean ones (e.g. gophers, moles). The upper fence is composed of four strands of tensioned wire strung at equal vertical intervals.

Sampling: Sampling of the experiments followed Borer et al. (2014b). In brief, in permanently designated subplots within each plot, primary productivity was estimated by clipping of all plants and litter rooted within two 0·1-m^2 strips (10 cm × 100 cm) for a total of 0·2 m^2. These samples were sorted to functional group (forb, grass, legumes, litter or previous year's growth), dried at 60 °C to constant mass and weighed to the nearest 0·01 g. Leaves and current year's woody growth were collected from any shrubs and subshrubs rooted in the plots. Areal cover was estimated to the nearest 1% for each species rooted in a 1m x 1m core subplot; cover estimates included woody overstory, litter, bare soil, rock and animal activity (e.g. digging). All measurements were collected at peak biomass at each site.

Arthropods were sampled from thirteen sites in the Nutrient Network (Table 1), selected by willingness of investigators to participate. Three sites were sampled in the first year following initiation of treatment, eight sites after two years, and two sites after three years (Table 1). Arthropods were vacuum-sampled with a leafblower modified to vacuum (Stewart and Wright 1995). Vacuum

sampling has several advantages over other leaf-sampling methods such as sweep-netting or hand-collecting in that it is quick, generally as good as other methods for sampling a variety of arthropod orders and samples consistently across vegetation types (Stewart and Wright 1995). A fine mesh (organza) bag was inserted into an extension on the vacuum sampler, and the sampler was run for 30 seconds over a 1m x 1m subplot, brushing the vegetation thoroughly ground to top. Sampled arthropods were promptly placed on ice and then kept frozen at -20C until processed. Further descriptions of the sites and arthropod sampling are provided in Appendix S1.

Sorting & Processing: Investigators at each site separated arthropods from plant material and other debris and then sorted as follows. Individuals were sorted into arthropod Orders as defined in Triplehorn and Johnson (2005). The following finer taxonomic groupings within Insecta were also separated: Hemiptera: Auchenorrhynca (hoppers), Hemiptera: Sternorrhyncha (aphids and scales), and Hymenoptera: Formicidae (ants). Arthropods smaller than 2mm in length were grouped and retained but not further identified.

The number of individuals in each arthropod classification for each plot was counted. Then groups were dried to a constant mass at 60C for at least two days, and weighed to the nearest 0.01 mg. Thus the total arthropod biomass and number of individuals was determined for each arthropod taxonomic group within each plot.

Statistical Analysis: We conducted separate analyses for the multiple-nutrient experiment and the fence-by-fertilization experiment. In each case we asked whether the treatments resulted in a change to secondary production. We evaluated the presence of these effects using linear mixed effects models where the response was the natural log of total arthropod biomass, the predictors were the factorial treatments, and the intercept was allowed to vary by site (the random effect). Initial models indicated

a block within site effect captured no variance, so this term was not used. These models were implemented in R 3.2 (R Core Team 2015) using the *nlme* package (Pinheiro et al. 2015).

In addition to these main effects, we investigated how the influence of soil nutrient availability and mammalian herbivory (treatments) was translated through the primary producer community to the arthropod community. Specifically, we used path analysis (a form of structural equation modeling without latent variables) to test potentially complementary hypotheses of the roles of plant productivity, diversity, physical structure, and composition on arthropod biomass. These potential pathways are depicted in Figure 1 (the metamodel, *sensu* Grace et al. 2010).

For the path analysis, we quantified the conceptual variables as follows. Plant structure was represented by the mass of thatch (i.e. previous years' plant production; g m^{-2}), plant biomass was measured as live plant biomass (g m^{-2}), plant diversity by the inverse Simpson's index based on the number and relative abundance of plant species (unitless). To address plant quality, we used two approaches because plant chemistry data were not available from all sites (Table 1). One path analysis was constructed using all 13 sites with a direct link from the nutrient and fencing treatments to the arthropod response variables; a significant path would indicate a missing plant community variable other than structure, diversity, or biomass. A second path analysis was then run using ten of the sites, for which data were available on carbon to nitrogen (C:N) ratio by mass of the leaves of the three to five most abundant plant species per plot. These data were collected in a different year than the arthropod sampling, thus they provide information on the foliar chemistry environment, but require the assumption that nutrient fertilization effects on foliar chemistry of these dominant species are consistent through time.

Arthropod body size was represented by the mean mass of an arthropod individual in each plot (mg). Arthropod number was measured as the simple count of individuals in each plot. Finally, the response variable of secondary production was quantified as total arthropod dry biomass (mg).

We used multilevel path analysis (Shipley 2009, 2013) to test our hypotheses in the metamodel. We implemented the model in R 3.2 (R Core Team 2015) using the package *piecewiseSEM* (Lefcheck

2015; full model code is shared online in Data S1). In this implementation mixed effects models are constructed separately for each predicted variable, and generalized forms (Poisson, binomial) can be used. The mixed effects models are then combined and tested with the d-separation test for goodness of fit (Shipley 2009) and path coefficients extracted from models which fit. We utilized a step-wise fitting procedure in which we first fit the model as specified in the metamodel, then added paths where necessary to achieve model fit, based on estimates of path strength. For instance, the metamodel does not contain direct links between treatment indicators and the arthropod responses, but in some cases these were necessary to achieve model fit. No paths were removed from the model. Variables were transformed to better meet assumptions of linearity: the arthropod, live plant and thatch mass variables, the diversity index, count of arthropod individuals and foliar C:N ratio were transformed by natural logarithm. We report standardized path coefficients incorporating site variation, *P* values as estimated from F-test of that path being dropped from the model using denominator degrees of freedom estimated by the Kenwood-Roger method (Lefcheck 2015), as well as the conditional and marginal R^2 (Nakagawa and Schielzeth 2013) for each downstream variable.

Results:

Total arthropod biomass per plot averaged 83.2 ± 5.7 mg m^{-2} (mean ± SE; range 1.2 – 1011.2) across the thirteen sites. Arthropod biomass across all sites was dominated by herbivores, specifically the Orthoptera (33.6% by mass), Auchenorrhyncha (20.1%), and Phasmatodea (16%). The Auchenorrhyncha dominated counts of individuals, comprising 33.9% of all individuals encountered across all plots and sites, followed by Acari (10%) and Diptera (8.7%). A full table of observed arthropods and their grouped masses per plot is included in Data S1.

Experimental addition of nitrogen increased arthropod consumer biomass by 38% on average (Figure 2a, Table 2). No other nutrient or combination of nutrients affected total consumer biomass. In the fence-by-fertilization experiment, addition of all nutrients increased arthropod consumer

biomass by a similar magnitude as nitrogen alone (43%), reflecting the main effect of nitrogen and a lack of interactive effects. While there was a trend toward decreased arthropod biomass inside fences (Figure 2b, Table 2), the main effect of fences and the interaction of fences and nutrients were not significantly different from zero.

Path analysis clarified the mechanisms producing the consumer biomass response to N addition (Table 3; Figure 3). The total mass of arthropods per plot was much more heavily influenced by the mean size of the individuals than the overall numbers of arthropods. Arthropod mean body size and abundance were positively correlated; however mean size was a much stronger predictor of overall secondary production than abundance. Crucially, the path model fit the data well (Fisher's C = 12.68, k = 16, P = 0.696), but only when direct paths were added from the nitrogen treatment indicator to both arthropod mean body size and abundance.

Experimental treatments altered plant biomass: addition of N and P led to higher plant live biomass, as did removal of mammalian herbivores with fencing. Plant live biomass and thatch were positively correlated, while live biomass and plant diversity were negatively correlated. Arthropod abundance increased with both plant live biomass and thatch, while higher plant live biomass led to lower mean arthropod size.

The model incorporating foliar nutrient data for 10 sites fit the data with similar paths and strengths as observed in the all-site model (Fisher's C = 45.35, k = 36, P = 0.137; Table 4, Figure 4). Addition of N and P led to higher plant live biomass. The main effect of N fertilization also significantly lowered mean foliar C:N ratios of the dominant plant species over the unfertilized plots (depicted as an increase in plant nutritional chemistry). These effects in turn acted through differential pathways to affect total consumer biomass. Arthropod abundance increased with increasing live plant

biomass, while arthropod mean size increased with lower plant foliar C:N (i.e., higher foliar nitrogen content). The number and mean size of the arthropods were positively correlated. Thus N addition indirectly supported both more, and bigger, arthropods through different intermediary aspects of the primary producer trophic level.

Discussion

The impacts on plant communities of altered soil nutrient supply and mammalian herbivory are bound to have effects in higher trophic levels, arising through multiple, occasionally opposing pathways which are not well understood. Here we demonstrate that across 13 diverse grassland ecosystems, nitrogen fertilization significantly increased biomass of arthropod consumers. Path analysis demonstrates that the increased secondary production was mediated through multiple pathways: through increases in arthropod abundance which were driven by increasing live plant biomass and thatch; and through increases in mean arthropod size driven by increasing foliar nitrogen content.

While both factors were similarly impacted by N additions, mean arthropod body size, not abundance, primarily accounted for the observed consumer biomass response (Borer et al. 2012). The positive covariance between arthropod body size and arthropod abundance also indicated increasing resources, rather than a tradeoff between size and number as might be expected under the energy equivalence rule (Carbone et al. 2007). The centrality of nitrogen in driving insect herbivory is a long-standing hypothesis (e.g., Mattson 1980, White 1984). Plant quality research in grasslands has focused therefore mostly on nutritional content, ratios, and macronutrient consumption in explaining insect herbivory (Cebrian et al. 2009, Hillebrand et al. 2009, Joern et al. 2011, Simpson et al. 2015). Nutritional limitations of plants can also cascade to higher trophic levels by limiting nutrient content of herbivorous prey (Fagan and Denno 2004, Wilder et al. 2013). Some recent evidence has pointed to potential co- or multiple-nutrient limitation of herbivores (Bishop et al. 2010, Joern et al. 2011, Kaspari et al. 2017). We found no evidence for co-limitation of secondary production in the 13

grasslands in which we conducted the multiple-nutrient experiment. Instead, nitrogen, alone or in concert with other nutrients, increased arthropod biomass.

Mammalian herbivory in the form of grazing has a diversity of potential effects on grassland arthropod communities (van Klink et al. 2015, Foster et al. 2014). In a meta-analysis, Foster et al. (2014) demonstrated high densities of large native herbivores typically decrease arthropod abundance and diversity. These impacts were explained through a variety of supposed mechanisms, direct and indirect, offered by the authors of the original studies used in the meta-analysis; still Foster et al. (2014) recommended untangling the potential pathways of influence from large herbivores through the primary producer community, which we attempt here.

Farrel et al. (2015) found grazing by cattle led to significantly higher arthropod biomass, especially in annual-dominated grasslands. Likewise, Moran (2014) showed grazing by bison in a prairie system increased arthropod biomass, especially earlier in the growing season.

One limitation of the present study is that we were only able to collect a single sample per plot at the end of the growing season, thus limiting interpretation of any potential seasonal dynamics. Nonetheless there was a marginal (P=0.07) decline in total arthropod biomass associated with the fencing treatment in our experiment, in agreement with the hypothesis that grazing stimulates increases in arthropod biomass. Two recent meta-analyses have indicated higher arthropod abundance (though without considering biomass) in areas with less or no large mammal herbivory (Foster et al. 2014; Tagaki and Miyashita 2014). The discrepancy between these results and ours may be explained by the type of arthropod community response metric, but it might also be due to the variable background levels of herbivory across sites in this study. Exclosure with fencing leads to comparable inside large animal herbivory (near zero), but against a variable background of mammalian grazing pressure outside the fences. Additionally, our path analysis did not contribute substantially to understanding the mechanism underlying a reduction of secondary production with fencing, as fencing only had a weakly positive effect on live plant mass, which in turn led to increases in arthropod abundance. A previous study replicated at 40 sites in the Nutrient Network found both

negative and positive mammalian herbivore effects on plant diversity, contingent locally on other factors, with a weak overall mean effect (Borer et al. 2014b). The direct influence of these herbivores on arthropod abundance, included as a direct path from the fencing treatment, was not significantly different from zero in either path analysis model.

Theory and previous empirical work suggest that secondary production should be mediated by plant diversity, productivity, and structure. With respect to plant diversity, we found no influence in either model on the abundance or mean size of arthropods and thus total arthropod biomass. One drawback to our "ecosystem entomology" approach is apparent here, in that diversity metrics (like the inverse Simpson's D which we use) capture changes in the number and evenness of species, but not their identity, which can mask important differences in e.g. nutritional content or defensive chemistry (Avolio et al. 2015). The change in identity of members of plant communities may strongly influence the abundance of herbivores and their natural enemies, even on the scale of meters (Lind et al. 2015). Thus a further analysis of this dataset might profitably focus on individual arthropod consumer groups and the beta diversity of both plants and arthropod consumers across plots in response to treatments.

Plant biomass played a central role mediating higher arthropod biomass as a response to increased soil nitrogen, but operated in unexpectedly opposing ways on the two aspects of the arthropod community. In the path analysis without foliar nutrient data (Figure 3), increasing plant live biomass in response to treatment led to higher abundance of arthropods, but the arthropods were of smaller mean size. Because both arthropod size and abundance contributed positively to the overall secondary production, this led to opposing effects of biomass through these two channels. Overall, the influence of plant biomass on arthropod biomass was actually slightly negative (summarizing paths [-0.185*0.876] + [0.146*0.332] = -0.114) due to the disproportionate effect of mean body size on secondary production. This result differs from a previous analysis that demonstrated strong positive influence of plant biomass on arthropod biovolume (Borer et al. 2012). However, plant biomass changes in Borer et al. (2012) were responses to manipulated plant diversity, rather to than nutrient

availability, as in this study, and experimental plots were burned annually, removing existing thatch and standing biomass. It is notable that in our analysis that included foliar nutrient data, the negative influence of plant biomass on mean size disappeared, while the positive influence on arthropod abundance remained (Figure 4).

Plant structure was represented in our analyses by the dry mass of thatch, admittedly an imperfect measure of structure (since live biomass provides most structure, and one site [Konza prairie] had little to no thatch due to burning). Despite these shortcomings, thatch as a surrogate for structure had a consistently positive effect on abundance of arthropods in both path analyses. This is consistent with prior work emphasizing the importance of physical structure in allowing predators and prey alike to find refuge (Finke and Denno 2002). An alternate hypothesis is that thatch increased the abundance of an additional functional group - detritivores. Collembola represented nearly 5% of individual arthropods in our samples, although composing a tiny fraction (0.1%) of arthropod biomass. We did not examine responses of individual orders within the path analysis framework, but a post-hoc bivariate examination of the relationship between Collembola abundance and thatch biomass showed no significant relationship ($F_{1,76}$=2.15, P=0.15).

We observed direct positive effects of the nitrogen addition treatment on both arthropod abundance and mean size, indicating effects on arthropods through the plant community after accounting for plant diversity, biomass, and structure. We ignore actual direct effects of fertilization on abundance or size of arthropods, though conceivably some could have congregated around or directly consumed the fertilizer. A likely mediator in the primary producer layer is foliar tissue composition in terms of nutrient concentration and defensive chemistry. Nutrient content of primary producers can mediate energy transfer across trophic levels and thus control secondary production (Mattson 1980, White 1984, Cebrian 1999, Kay et al. 2005, Kaspari et al. 2017). Empirical evidence has shown that foliar N concentration is the best predictor of host plant quality for many herbivorous arthropods, strongly

affecting growth, survivorship, and reproduction rates (Throop et al. 2004, Hillebrand and Lehmpfuhl 2011). In addition to plant nutrient content, structural and chemical defenses also influence palatability to herbivores. Plant allocation to defense depends in some systems on environmental nutrient availability (Throop et al. 2004), where investment by plants in defensive compounds may be reduced in resource-rich environments (Fine et al. 2006). Additionally, plant species responses to nutrient addition tend to correlate positively with plant responses to mammalian herbivore removal (Lind et al. 2013), indicating a shift to a strategy based on less well-defended tissues with increased foliar nutrient concentrations.

While we have no data on the defensive chemistry of these plants, the high rates of N added in our experimental treatment do increase plant tissue %N content (Figure 4, (La Pierre and Smith 2015)). The path analysis including foliar C:N data supports the idea that this increase in stoichiometric balance towards N leads to more consumer biomass, specifically by increasing mean size of arthropods. In our dataset herbivores are the majority of higher biomass individuals, thus this path suggests the main influence of increased nutrient availability on consumer biomass is mediated by a shift towards larger herbivores due to increased nutritional content of plant tissue. An open question is whether increases in consumer biomass represent a numerical response (congregation, or increase in abundance) or a developmental response (size changes due to improved nutrition). While we observed changes in mean size due to increased foliar %N, this could have been a function of choice by larger herbivores, as has been demonstrated in other grassland fertilization experiments (Loaiza et al. 2011).

The response we observed has important implications for the functional role of arthropods in these grassland ecosystems. Arthropods can have important effects on plant community composition, biomass, and C storage (Throop et al. 2004, Blue et al. 2011, La Pierre et al 2015). Metabolic theory suggests that herbivore body size is a predictor of per-capita rates of herbivory across species (Brown et al. 2004), and empirical evidence supports this (Hillebrand et al. 2009). However abundance is not

always a reliable predictor of effective herbivory rates, because arthropod herbivores may consume less tissue if their nutritional needs can be met with fewer bites (La Pierre and Smith 2016) or increased abundance is driven by small-bodied consumers (Gruner and Taylor 2006). Finally, where arthropods remain local to the system there can be significant positive feedbacks in increased arthropod density to the nutrients available to the primary producers (Yang and Gratton 2014).

Conclusions. Eutrophication, in particular terrestrial nitrogen deposition, and alterations of large herbivore communities are pervasive features of the Anthropocene. Here we demonstrate that one consequence of increased nitrogen availability is increased arthropod secondary production, mediated by changes in the plant community including physical structure, live biomass, and especially foliar nutritional composition. Grazing by wild mammalian herbivores had relatively little consequence for arthropod biomass, though the rates of the grazing activity in the natural grasslands under study varied. Consumer biomass was driven largely by the mean size of consumers, which responded positively to increased foliar nitrogen. There were negligible effects of mammalian herbivores on arthropod consumers in either direct or indirect paths. Together these results indicate that unintentional changes to environmental conditions of natural grasslands will cascade in predictable ways to the consumer community, yielding as yet uncertain impacts on ecosystem function.

Acknowledgments

We acknowledge the contribution of Nutrient Network investigators who collected plant data used in this manuscript. We especially appreciate the sampling design and methodology developed for this project by Elizabeth M. Wolkovich. This work was generated using data from the Nutrient Network (http://www.nutnet.org) experiment, funded at the site-scale by individual researchers. Coordination and data management have been supported by funding to E. Borer and E. Seabloom from the National Science Foundation Research Coordination Network (NSF-DEB-1042132) and Long Term Ecological Research (NSF-DEB-1234162 to Cedar Creek LTER) programs, and the Institute on the Environment

(DG-0001-13). We also thank the Minnesota Supercomputer Institute for hosting project data and the Institute on the Environment for hosting Network meetings

Literature Cited

Avolio, M. L., K. J. L. Pierre, G. R. Houseman, S. E. Koerner, E. Grman, F. Isbell, D. S. Johnson, and K. R. Wilcox. 2015. A framework for quantifying the magnitude and variability of community responses to global change drivers. Ecosphere 6:1–14.

Awmack, C. S., and S. R. Leather. 2002. Host plant quality and fecundity in herbivorous insects. Annual Review of Entomology 47:817–844.

Bakker, E. S., M. E. Ritchie, H. Olff, D. G. Milchunas, and J. M. H. Knops. 2006. Herbivore impact on grassland plant diversity depends on habitat productivity and herbivore size. Ecology Letters 9:780–788.

Bishop, J. G., N. B. O'Hara, J. H. Titus, J. L. Apple, R. A. Gill, and L. Wynn. 2010. N-P co-limitation of primary production and response of arthropods to N and P in early primary succession on Mount St. Helens volcano. Plos One 5.

Blue, J. D., L. Souza, A. T. Classen, J. A. Schweitzer, and N. J. Sanders. 2011. The variable effects of soil nitrogen availability and insect herbivory on aboveground and belowground plant biomass in an old-field ecosystem. Oecologia 167:771.

Borer, E. T., W. S. Harpole, P. B. Adler, E. M. Lind, J. L. Orrock, E. W. Seabloom, and M. D. Smith. 2014a. Finding generality in ecology: a model for globally distributed experiments. Methods in Ecology and Evolution 5:65–+.

Borer, E. T., E. W. Seabloom, D. S. Gruner, W. S. Harpole, H. Hillebrand, E. M. Lind, P. B. Adler, J. Alberti, T. M. Anderson, J. D. Bakker, L. Biederman, D. Blumenthal, C. S. Brown, L. A. Brudvig, Y. M. Buckley, M. Cadotte, C. Chu, E. E. Cleland, M. J. Crawley, P. Daleo, E. I.

Damschen, K. F. Davies, N. M. DeCrappeo, G. Du, J. Firn, Y. Hautier, R. W. Heckman, A. Hector, J. HilleRisLambers, O. Iribarne, J. A. Klein, J. M. H. Knops, K. J. La Pierre, A. D. B. Leakey, W. Li, A. S. MacDougall, R. L. McCulley, B. A. Melbourne, C. E. Mitchell, J. L. Moore, B. Mortensen, L. R. O'Halloran, J. L. Orrock, J. Pascual, S. M. Prober, D. A. Pyke, A. C. Risch, M. Schuetz, M. D. Smith, C. J. Stevens, L. L. Sullivan, R. J. Williams, P. D. Wragg, J. P. Wright, and L. H. Yang. 2014b. Herbivores and nutrients control grassland plant diversity via light limitation. Nature 508:517–+.

Borer, E. T., E. W. Seabloom, and D. Tilman. 2012. Plant diversity controls arthropod biomass and temporal stability. Ecology Letters 15:1457–1464.

Brown, J. H., J. F. Gillooly, A. P. Allen, V. M. Savage, and G. B. West. 2004. Toward a metabolic theory of ecology. Ecology 85:1771–1789.

Carbone, C., J. M. Rowcliffe, G. Cowlishaw, and N. J. B. Isaac. 2007. The scaling of abundance in consumers and their resources: implications for the energy equivalence rule. American Naturalist 170:479–484.

Cebrian, J. 1999. Patterns in the fate of production in plant communities. American Naturalist 154:449–468.

Cebrian, J. 2004. Role of first- order consumers in ecosystem carbon flow. Ecology Letters 7:232–240.

Cebrian, J. 2015. Energy flows in ecosystems. Science 349:1053–1054.

Clark, C. M., and D. Tilman. 2008. Loss of plant species after chronic low-level nitrogen deposition to prairie grasslands. Nature 451:712–715.

Elser, J. J., M. E. S. Bracken, E. E. Cleland, D. S. Gruner, W. S. Harpole, H. Hillebrand, J. T. Ngai, E. W. Seabloom, J. B. Shurin, and J. E. Smith. 2007. Global analysis of nitrogen and phosphorus limitation of primary producers in freshwater, marine and terrestrial ecosystems. Ecology

Letters 10:1135–1142.

Fagan, W. F., and R. F. Denno. 2004. Stoichiometry of actual vs. potential predator-prey interactions: insights into nitrogen limitation for arthropod predators. Ecology Letters 7:876–883.

Farrell, K. A., W. S. Harpole, C. Stein, K. N. Suding, and E. T. Borer. 2015. Grassland Arthropods Are Controlled by Direct and Indirect Interactions with Cattle but Are Largely Unaffected by Plant Provenance. PLoS ONE 10:e0129823.

Fay, P. A., S. M. Prober, W. S. Harpole, J. M. H. Knops, J. D. Bakker, E. T. Borer, E. M. Lind, A. S. MacDougall, E. W. Seabloom, P. D. Wragg, P. B. Adler, D. M. Blumenthal, Y. M. Buckley, C. Chu, E. E. Cleland, S. L. Collins, K. F. Davies, G. Du, X. Feng, J. Firn, D. S. Gruner, N. Hagenah, Y. Hautier, R. W. Heckman, V. L. Jin, K. P. Kirkman, J. Klein, L. M. Ladwig, Q. Li, R. L. McCulley, B. A. Melbourne, C. E. Mitchell, J. L. Moore, J. W. Morgan, A. C. Risch, M. Schütz, C. J. Stevens, D. A. Wedin, and L. H. Yang. 2015. Grassland productivity limited by multiple nutrients. Nature Plants 1:15080.

Fine, P. V. A., Z. J. Miller, I. Mesones, S. Irazuzta, H. M. Appel, M. H. H. Stevens, I. Saaksjarvi, L. C. Schultz, and P. D. Coley. 2006. The growth-defense trade-off and habitat specialization by plants in Amazonian forests. Ecology 87:S150–S162.

Finke, D., and R. Denno. 2002. Intraguild predation diminished in complex-structured vegetation: Implications for prey suppression. Ecology 83:643–652.

Foster, C. N., P. S. Barton, and D. B. Lindenmayer. 2014. Effects of large native herbivores on other animals. Journal of Applied Ecology 51:929–938.

Grace, J. B., T. M. Anderson, H. Olff, and S. M. Scheiner. 2010. On the specification of structural equation models for ecological systems. Ecological Monographs 80:67–87.

Gruner, D. S., and A. D. Taylor. 2006. Richness and species composition of arboreal arthropods affected by nutrients and predators: a press experiment. Oecologia 147:714–724.

Haddad, N., G. Crutsinger, K. Gross, J. Haarstad, J. Knops, and D. Tilman. 2009. Plant species loss decreases arthropod diversity and shifts trophic structure. Ecology Letters 12:1029–1039.

Harpole, W. S., L. L. Sullivan, E. M. Lind, J. Firn, P. B. Adler, E. T. Borer, J. Chase, P. A. Fay, Y. Hautier, H. Hillebrand, A. S. MacDougall, E. W. Seabloom, R. Williams, J. D. Bakker, M. W. Cadotte, E. J. Chaneton, C. Chu, E. E. Cleland, C. D'Antonio, K. F. Davies, D. S. Gruner, N. Hagenah, K. Kirkman, J. M. H. Knops, K. J. La Pierre, R. L. McCulley, J. L. Moore, J. W. Morgan, S. M. Prober, A. C. Risch, M. Schuetz, C. J. Stevens, and P. D. Wragg. 2016. Addition of multiple limiting resources reduces grassland diversity. Nature 537:93–96.

Harpole, W., and D. Tilman. 2007. Grassland species loss resulting from reduced niche dimension. Nature 446:791–793.

Hillebrand, H., E. T. Borer, M. E. S. Bracken, B. J. Cardinale, J. Cebrian, E. E. Cleland, J. J. Elser, D. S. Gruner, W. S. Harpole, J. T. Ngai, S. Sandin, E. W. Seabloom, J. B. Shurin, J. E. Smith, and M. D. Smith. 2009. Herbivore metabolism and stoichiometry each constrain herbivory at different organizational scales across ecosystems. Ecology Letters 12:516–527.

Hillebrand, H., and V. Lehmpfuhl. 2011. Resource Stoichiometry and Consumers Control the Biodiversity-Productivity Relationship in Pelagic Metacommunities. The American Naturalist 178:171–181.

Janssen, A., M. W. Sabelis, S. Magalhães, M. Montserrat, and T. van der Hammen. 2007. Habitat structure affects intraguild predation. Ecology 88:2713–2719.

Joern, A., T. Provin, and S. T. Behmer. 2011. Not just the usual suspects: Insect herbivore populations and communities are associated with multiple plant nutrients. Ecology 93:1002–1015.

Kaspari, M., K. A. Roeder, B. Benson, M. D. Weiser, and N. J. Sanders. 2017. Sodium co-limits and catalyzes macronutrients in a prairie food web. Ecology 98:315–320.

Kay, A., I. Ashton, E. Gorokhova, A. Kerkhoff, A. Liess, and E. Litchman. 2005. Toward a

stoichiometric framework for evolutionary biology. Oikos 109:6–17.

van Klink, R., F. van der Plas, C. G. E. (Toos) van Noordwijk, M. F. WallisDeVries, and H. Olff. 2015. Effects of large herbivores on grassland arthropod diversity. Biological Reviews 90:347–366.

Knapp, A. K., J. M. Blair, J. M. Briggs, S. L. Collins, D. C. Hartnett, L. C. Johnson, and E. G. Towne. 1999. The Keystone Role of Bison in North American Tallgrass Prairie: Bison increase habitat heterogeneity and alter a broad array of plant, community, and ecosystem processes. BioScience 49:39–50.

La Pierre, K. J. L., and M. D. Smith. 2015. Soil nutrient additions increase invertebrate herbivore abundances, but not herbivory, across three grassland systems. Oecologia:1–13.

LeBauer, D. S., and K. K. Treseder. 2008. Nitrogen limitation of net primary productivity in terrestrial ecosystems is globally distributed. Ecology 89:371–379.

Lefcheck, J. S. 2015. piecewiseSEM: Piecewise structural equation modeling in R for ecology, evolution, and systematics. arXiv:1509.01845.

Lind, E. M., E. Borer, E. Seabloom, P. Adler, J. D. Bakker, D. M. Blumenthal, M. Crawley, K. Davies, J. Firn, D. S. Gruner, W. S. Harpole, Y. Hautier, H. Hillebrand, J. Knops, B. Melbourne, B. Mortensen, A. C. Risch, M. Schuetz, C. Stevens, and P. D. Wragg. 2013. Life-history constraints in grassland plant species: a growth-defence trade-off is the norm. Ecology Letters 16:513–521.

Lind, E. M., J. B. Vincent, G. D. Weiblen, J. Cavender-Bares, and E. T. Borer. 2015. Trophic phylogenetics: evolutionary influences on body size, feeding, and species associations in grassland arthropods. Ecology 96:998–1009.

Loaiza, V., J. L. Jonas, and A. Joern. 2011. Grasshoppers (Orthoptera: Acrididae) select vegetation patches in local- scale responses to foliar nitrogen but not phosphorus in native grassland.

Insect Science 18:533–540.

Mattson, W. 1980. Herbivory in relation to plant nitrogen content. Annual Review of Ecology and Systematics 11:119–161.

McNaughton, S. J. 1984. Grazing Lawns - Animals in Herds, Plant Form, and Coevolution. American Naturalist 124:863–886.

McNaughton, S. J., M. Oesterheld, D. A. Frank, and K. J. Williams. 1989. Ecosystem-level patterns of primary productivity and herbivory in terrestrial habitats. Nature 341:142–144.

Moran, M. D. 2014. Bison Grazing Increases Arthropod Abundance and Diversity in a Tallgrass Prairie. Environmental Entomology 43:1174–1184.

Nakagawa, S., and H. Schielzeth. 2013. A general and simple method for obtaining R2 from generalized linear mixed-effects models. Methods in Ecology and Evolution 4:133–142.

Olff, H., and D. M. Pegtel. 1994. Characterisation of the type and extent of nutrient limitation in grassland vegetation using a bioassay with intact sods. Plant and Soil 163:217–224.

Pinheiro J, Bates D, DebRoy S, Sarkar D and R Core Team (2017). _nlme: Linear and Nonlinear Mixed Effects Models_. R

package version 3.1-131, <URL: https://CRAN.R-project.org/package=nlme>.Poelman, E. H., J. J. A. van Loon, and M. Dicke. 2008. Consequences of variation in plant defense for biodiversity at higher trophic levels. Trends in Plant Science 13:534–541.

Polis, G. A., W. B. Anderson, and R. D. Holt. 1997. TOWARD AN INTEGRATION OF LANDSCAPE AND FOOD WEB ECOLOGY:The Dynamics of Spatially Subsidized Food Webs. Annual Review of Ecology and Systematics 28:289–316.

Rockstrom, J., W. Steffen, K. Noone, A. Persson, F. S. Chapin, E. F. Lambin, T. M. Lenton, M. Scheffer, C. Folke, H. J. Schellnhuber, B. Nykvist, C. A. de Wit, T. Hughes, S. van der Leeuw, H. Rodhe, S. Sorlin, P. K. Snyder, R. Costanza, U. Svedin, M. Falkenmark, L.

Karlberg, R. W. Corell, V. J. Fabry, J. Hansen, B. Walker, D. Liverman, K. Richardson, P. Crutzen, and J. A. Foley. 2009. A safe operating space for humanity. Nature 461:472–475.

Rzanny, M., A. Kuu, and W. Voigt. 2012. Bottom–up and top–down forces structuring consumer communities in an experimental grassland. Oikos:no–no.

Scherber, C., N. Eisenhauer, W. W. Weisser, B. Schmid, W. Voigt, M. Fischer, E.-D. Schulze, C. Roscher, A. Weigelt, E. Allan, H. Beßler, M. Bonkowski, N. Buchmann, F. Buscot, L. W. Clement, A. Ebeling, C. Engels, S. Halle, I. Kertscher, A.-M. Klein, R. Koller, S. König, E. Kowalski, V. Kummer, A. Kuu, M. Lange, D. Lauterbach, C. Middelhoff, V. D. Migunova, A. Milcu, R. Müller, S. Partsch, J. S. Petermann, C. Renker, T. Rottstock, A. Sabais, S. Scheu, J. Schumacher, V. M. Temperton, and T. Tscharntke. 2010. Bottom-up effects of plant diversity on multitrophic interactions in a biodiversity experiment. Nature 468:553–556.

Schrama, M., P. Heijning, J. P. Bakker, H. J. van Wijnen, M. P. Berg, and H. Olff. 2013. Herbivore trampling as an alternative pathway for explaining differences in nitrogen mineralization in moist grasslands. Oecologia 172:231–243.

Seabloom, E. W., E. T. Borer, Y. Buckley, E. E. Cleland, K. Davies, J. Firn, W. S. Harpole, Y. Hautier, E. Lind, A. Macdougall, J. L. Orrock, S. M. Prober, P. Adler, J. Alberti, T. M. Anderson, J. D. Bakker, L. A. Biederman, D. Blumenthal, C. S. Brown, L. A. Brudvig, M. Caldeira, C. Chu, M. J. Crawley, P. Daleo, E. I. Damschen, C. M. D'Antonio, N. M. Decrappeo, C. R. Dickman, G. Du, P. A. Fay, P. Frater, D. S. Gruner, N. Hagenah, A. Hector, A. Helm, H. Hillebrand, K. S. Hofmockel, H. C. Humphries, O. Iribarne, V. L. Jin, A. Kay, K. P. Kirkman, J. A. Klein, J. M. H. Knops, K. J. La Pierre, L. M. Ladwig, J. G. Lambrinos, A. D. B. Leakey, Q. Li, W. Li, R. Mcculley, B. Melbourne, C. E. Mitchell, J. L. Moore, J. Morgan, B. Mortensen, L. R. O'Halloran, M. Paertel, J. Pascual, D. A. Pyke, A. C. Risch, R. Salguero-Gomez, M. Sankaran, M. Schuetz, A. Simonsen, M. Smith, C. Stevens, L. Sullivan, G. M. Wardle, E. M. Wolkovich, P. D. Wragg, J. Wright, and L. Yang. 2013. Predicting invasion in grassland ecosystems: is exotic dominance the real embarrassment of richness?

GLOBAL CHANGE BIOLOGY 19:3677–3687.

Shipley, B. 2009. Confirmatory path analysis in a generalized multilevel context. Ecology 90:363–368.

Shipley, B. 2013. The AIC model selection method applied to path analytic models compared using a d-separation test. Ecology 94:560–564.

Steffen, W., K. Richardson, J. Rockström, S. E. Cornell, I. Fetzer, E. M. Bennett, R. Biggs, S. R. Carpenter, W. de Vries, C. A. de Wit, C. Folke, D. Gerten, J. Heinke, G. M. Mace, L. M. Persson, V. Ramanathan, B. Reyers, and S. Sörlin. 2015. Planetary boundaries: Guiding human development on a changing planet. Science:1259855.

Stevens, C. J., E. M. Lind, Y. Hautier, W. S. Harpole, E. T. Borer, S. Hobbie, E. W. Seabloom, L. Ladwig, J. D. Bakker, C. Chu, S. Collins, K. F. Davies, J. Firn, H. Hillebrand, K. J. L. Pierre, A. MacDougall, B. Melbourne, R. L. McCulley, J. Morgan, J. L. Orrock, S. M. Prober, A. C. Risch, M. Schuetz, and P. D. Wragg. 2015. Anthropogenic nitrogen deposition predicts local grassland primary production worldwide. Ecology 96:1459–1465.

Stewart, A., and A. Wright. 1995. A new inexpensive suction apparatus for sampling arthropods in grassland. Ecological Entomology 20:98–102.

Takagi, S., and T. Miyashita. 2014. Scale and system dependencies of indirect effects of large herbivores on phytophagous insects: a meta-analysis. Population Ecology 56:435–445.

R Development Core Team. 2017. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Throop, H., and M. Lerdau. 2004. Effects of nitrogen deposition on insect herbivory: Implications for community and ecosystem processes. Ecosystems 7:109–133.

Triplehorn, C., and N. Johnson. 2005. Borror and DeLong's Introduction to the Study of Insects. 7th edition. Thomson Brooks/Cole.

Tscharntke, T., and H. Greiler. 1995. Insect Communities, Grasses, and Grasslands. Annual Review of Entomology 40:535–558.

White, T. C. R. 1984. The abundance of invertebrate herbivores in relation to the availability of nitrogen in stressed food plants. Oecologia 63:90–105.

Wilder, S. M., M. Norris, R. W. Lee, D. Raubenheimer, and S. J. Simpson. 2013. Arthropod food webs become increasingly lipid-limited at higher trophic levels. Ecology Letters 16:895–902.

Wimp, G. M., S. M. Murphy, D. L. Finke, A. F. Huberty, and R. F. Denno. 2010. Increased primary production shifts the structure and composition of a terrestrial arthropod community. Ecology 91:3303–3311.

Yang, L. H., and C. Gratton. 2014. Insects as drivers of ecosystem processes. Current Opinion in Insect Science 2:26–32.

Table 1. Sites in this study.

site_code	site_name	region	country	year_trt	C:N data
bnch.us	Bunchgrass (Andrews LTER)	Montane West (North America)	US	3	Y
cbgb.us	Chichaqua Bottoms	Central plains (North America)	US	1	Y
cdcr.us	Cedar Creek LTER	Central plains (North America)	US	2	N
hopl.us	Hopland REC	Pacific Coast (North America)	US	3	Y
konz.us	Konza LTER	Central plains (North America)	US	2	Y
look.us	Lookout (Andrews LTER)	Montane West (North America)	US	2	Y
marc.ar	Mar Chiquita	Atlantic Coast (South America)	AR	1	N
mcla.us	Mclaughlin UCNRS	Pacific Coast (North America)	US	2	Y
sage.us	Sagehen Creek UCNRS	Montane West (North America)	US	1	Y
saline.us	Saline Experimental Range	Central plains (North America)	US	2	N
sgs.us	Shortgrass Steppe LTER	Central plains (North America)	US	2	Y
sier.us	Sierra Foothills REC	Pacific Coast (North America)	US	2	Y
unc.us	Duke Forest	Atlantic Coast (North America)	US	2	Y

Table 2. Analysis of deviance tables for linear mixed effects models examining change in arthropod biomass under the factorial nutrient addition experiment, and the all nutrients by fence experiment. Intercepts were allowed to vary by site (the random effect).

	Effect	X^2	Df	*P*
N	**0.324**	**10.365**	**1**	**0.001**
P	-0.109	0.400	1	0.527
K	0.167	0.310	1	0.578
N:P	0.064	1.164	1	0.281
N:K	-0.234	0.138	1	0.710
P:K	-0.165	0.001	1	0.978
N:P:K	0.319	0.594	1	0.441
NPK	**0.357**	**7.616**	**1**	**0.006**
fence	-0.397	3.242	1	0.072
NPK:fence	0.208	0.399	1	0.528

Table 3. Parameter estimates from path analysis for 13 site model displayed in Figure 3. Paths with strengths significantly different from zero are highlighted in bold.

Paths

Response and predictor	Effect Size	SE	*P*
Arthropod mass			
Number Arthropods	**0.332**	**0.018**	**<0.001**
Mean Size	**0.876**	**0.011**	**<0.001**
Number Arthropods			
Plant Mass	**0.146**	**0.059**	**0.013**
Plant Diversity	-0.001	0.036	0.987
Thatch	**0.209**	**0.068**	**0.002**
Fence	0.004	0.028	0.886
N	**0.112**	**0.030**	**0.000**
P	-0.017	0.029	0.554
K	-0.037	0.029	0.203
Mean Size Arthropods			
Plant Mass	**-0.185**	**0.088**	**0.035**
Plant Diversity	0.043	0.060	0.468
Thatch	0.059	0.094	0.535
N	**0.155**	**0.052**	**0.003**
P	-0.008	0.051	0.878
K	0.043	0.050	0.396
Plant Mass			
N	**0.145**	**0.027**	**0.000**
P	**0.094**	**0.027**	**0.001**
K	-0.019	0.027	0.478
Fence	**0.065**	**0.026**	**0.013**
Plant Diversity			

N	-0.052	0.045	0.246
P	-0.043	0.045	0.333
K	-0.001	0.045	0.981
Fence	0.013	0.043	0.770
Thatch			
N	-0.001	0.023	0.955
P	0.040	0.023	0.090
K	0.010	0.024	0.682
Fence	0.028	0.023	0.209

Covariances

Variable 1	Variable 2	Covariance	*P*
Number Arthropods	Mean Size	0.215	0.015
Plant Diversity	Thatch	-0.204	1.00
Plant Diversity	Plant Mass	-0.145	0.997
Plant Mass	Thatch	0.019	0.363

Notes: For each response, R^2_M values represent the marginal combined explanatory power of all predictor paths for that response, and the R^2_C values represent the conditional explanatory power of all predictor paths for that response, which include site random effects: arthropod mass, $R^2_M = 0.95$, $R^2_C = 0.97$; number arthropods, $R^2_M = 0.08$, $R^2_C = 0.75$; mean size arthropods, $R^2_M = 0.06$, $R^2_C = 0.25$; plant mass, $R^2_M = 0.04$, $R^2_C = 0.75$; plant diversity, $R^2_M = 0.01$, $R^2_C = 0.39$; thatch, $R^2_M = 0.00$, $R^2_C = 0.83$.

Table 4. Parameter estimates from path analysis for 10 site model displayed in Figure 4. Paths with strengths significantly different from zero are highlighted in bold.

Paths

Response and predictor	Effect Size	SE	*P*
Arthropod mass			
Number Arthropods	**0.358**	**0.027**	**<0.001**
Mean Size	**0.841**	**0.016**	**<0.001**
Number Arthropods			
Plant Mass	**0.114**	**0.045**	**0.018**
Plant Diversity	-0.021	0.044	0.582
Thatch	**0.185**	**0.074**	**0.013**
Fence	0.049	0.032	0.122
N	**0.092**	**0.037**	**0.014**
Foliar C:N	0.077	0.060	0.200
Mean Size Arthropods			
Plant Mass	-0.112	0.077	0.150
Plant Diversity	-0.067	0.079	0.402
Thatch	0.036	0.116	0.756
Foliar C:N	**-0.226**	**0.092**	**0.014**
Plant Mass			
N	**0.182**	**0.051**	**0.000**
P	**0.125**	**0.050**	**0.014**
K	-0.048	0.051	0.344
Fence	0.074	0.048	0.128
Plant Diversity			
N	-0.088	0.052	0.091
P	-0.041	0.051	0.427
K	0.009	0.052	0.862

Fence	0.040	0.049	0.412
Mean foliar C:N			
N	**-0.267**	**0.037**	**<0.001**
P	-0.056	0.037	0.131
K	0.044	0.038	0.245
Fence	-0.036	0.036	0.317
Thatch			
N	-0.009	0.030	0.770
P	0.027	0.030	0.373
K	0.022	0.030	0.465
Fence	0.003	0.029	0.914

Covariances

Variable 1	Variable 2	Covariance	*P*
Number Arthropods	Mean Size	0.265	<0.001
Foliar C:N	Plant Mass	0.353	<0.001
Plant Diversity	Plant Mass	-0.159	0.991
Plant Mass	Thatch	0.038	0.284

Notes: For each response, R^2_M values represent the marginal combined explanatory power of all predictor paths for that response, and the R^2_C values represent the conditional explanatory power of all predictor paths for that response, which include site random effects: arthropod mass, $R^2_M = 0.94$, $R^2_C = 0.96$; number arthropods, $R^2_M = 0.06$, $R^2_C = 0.81$; mean size arthropods, $R^2_M = 0.07$, $R^2_C = 0.31$; plant mass, $R^2_M = 0.05$, $R^2_C = 0.52$; plant diversity, $R^2_M = 0.01$, $R^2_C = 0.49$; mean foliar C:N, $R^2_M = 0.07$, $R^2_C = 0.76$; thatch, $R^2_M = 0.00$, $R^2_C = 0.83$.

Figure Legends

Figure 1. Metamodel used as basis for evaluating links between soil nutrient availability, mammalian herbivory, and consumer biomass. Hypothesized sign of influence is indicated. Gray boxes indicate factors manipulated in the experiment to alter the connected variable. Double-headed arrow indicates covariance between arthropod body size and number; similar covariances among all plant response variables were included in the analysis but not displayed in the metamodel for clarity. Letters indicating paths correspond to hypotheses discussed in the main text.

Figure 2: Effects of (a) soil nutrient availability and (b) mammalian herbivore removal and their interaction on arthropod biomass. Points are modeled estimates of mean log biomass per meter squared, error bars represent standard error of model estimates.

Figure 3. Path analysis of the response of arthropod biomass to manipulations of soil nutrients and mammalian herbivory. Overall model Fisher's C = 12.68, k = 16, P = 0.696. Paths with effects significantly different from zero using corrected p-values are drawn in width in proportion to their strength as either positive (solid line) or negative (dashed line) in sign. Double-headed arrows represent modeled covariances. Effect sizes of all paths and their significance are presented in Table 2. Variables are all per-plot, as follows: +N,+P,+K,+fence = indicator of treatment; plant diversity = Inverse Simpson's diversity index of plant community; plant biomass = live plant biomass in g m^{-2}; plant structure = mass of thatch in g m^{-2}; arthropod abundance = number of arthropods; arthropod body size = per capita mean mass of arthropods; 2° production = total arthropod biomass.

Figure 4. Path analysis of the response of arthropod biomass to manipulations of soil nutrients and mammalian herbivory, including data for plant biochemical composition. Overall model Fisher's C = 41.67, k = 34, P = 0.172. Paths with effects significantly different from zero using corrected p-values are drawn in width in proportion to their strength as either positive (solid line) or negative (dashed line) in sign. Double-headed arrows represent modeled covariances. Effect sizes of all paths and their significance are presented in Table 4. Variables are all per-plot, as follows: +N,+P,+K,+fencing = indicator of treatment; plant diversity = Inverse Simpson's diversity index of plant community; plant

biomass = live plant biomass in g m^{-2}; plant structure = mass of thatch in g m^{-2}; plant quality = negative mean foliar C:N ratio of dominant plant species; arthropod abundance = number of arthropods; arthropod body size = per capita mean mass of arthropods; 2° production = total arthropod biomass.